

Results from the U.S. EPA's Biological Open Water Surveillance Program of the Laurentian Great Lakes: I. Introduction and Phytoplankton Results

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ABSTRACT. *The Great Lakes National Program Office of the U.S. EPA has been conducting biological monitoring of the Laurentian Great Lakes since 1983. This paper presents synoptic survey data of phytoplankton communities from all five lakes. These communities were highly diverse, each lake typically supporting over 100 species during both the spring and summer surveys. Much of that diversity was contributed by diatoms, which dominated the plankton of all lakes except Lake Superior in the spring. Summer communities shifted away from diatoms, toward chrysophytes in the upper lakes and chlorophytes in the lower lakes. Ordination analyses indicated the close similarity of communities in the upper lakes, in particular Lakes Huron and Michigan, and a diverse range of communities in Lake Erie. Floristically, Lake Ontario was fundamentally different from all other lakes.*

INDEX WORDS: *Phytoplankton, ecology, ordination, diatoms.*

INTRODUCTION

The Laurentian Great Lakes constitute the largest continuous mass of fresh water on earth, and with a volume of 24,620 km³ (Wetzel 1983), contain nearly 20% of the world's unfrozen fresh water. These lakes represent an enormous cultural and economic resource for both the United States and Canada. Increasing population and industrial growth in recent history, however, has produced a trend of increasing eutrophication and raised concerns about declining water quality in the lakes. As a result of these concerns, in 1972 the United States and Canada signed the Great Lakes Water Quality Agreement as an expression of each country's commitment to restore and maintain the chemical, physical, and biological integrity of the Great Lakes basin ecosystem.

The Great Lakes National Program Office (GLNPO) of the United States Environmental Pro-

tection Agency (U.S. EPA) has primary responsibility within the U.S. for conducting surveillance monitoring of the offshore waters of the Great Lakes. This monitoring is intended to fulfill the provisions of the Great Lakes Water Quality Agreement (International Joint Commission 1978) calling for periodic monitoring of the lakes to: 1) assess compliance with jurisdictional control requirements; 2) provide information on non-achievement of agreed upon water quality objectives; 3) evaluate water quality trends over time; and 4) identify emerging problems in the Great Lakes basin ecosystem. The monitoring effort is focused on whole lake responses to changes in loadings of anthropogenic substances, so sampling is largely restricted to the relatively homogeneous offshore waters of each lake. Because of the daunting logistical exigencies of sampling such a large area, temporal resolution is currently limited to two well-defined periods during the year: the spring

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isothermal period and the stable, stratified summer period.

Monitoring of the Great Lakes by the GLNPO began in 1983, with coverage at that time including Lakes Michigan, Huron, and Erie. Initially Lakes Ontario and Superior were excluded from monitoring because the former was already monitored annually by Canada, and the latter was not felt to be susceptible to eutrophication. In 1986 sampling was extended to include Lake Ontario, and in 1992 sampling of Lake Superior was added. In addition to a wide range of physical and chemical parameters, the lakes have been sampled for phytoplankton and zooplankton, including crustaceans and rotifers, since the inception of the program. In 1997, a benthic invertebrate biomonitoring program was added to complement the existing open water surveillance sampling. This sampling program is unique in that all five lakes are sampled at essentially the same time by one agency, and samples are analyzed by one primary lab. Consequently, analytical methods, and most importantly taxonomy, remain consistent both over time and across all five lakes.

In this series of papers we will present results of the GLNPO biological surveillance sampling program from 1998. This represents the first time that biological data from all five Laurentian Great Lakes have been reported from the program. The goals in this series of papers are threefold: 1) to provide a general description of the offshore planktonic and the benthic communities of all five Great Lakes; 2) to identify large-scale patterns of distribution of these communities; and 3) to identify the potential physical and chemical factors controlling the species makeup of these communities. This paper deals with epilimnetic phytoplankton distribution and abundance. Other papers will address the occurrence of deep phytoplankton communities in the summer and the distribution and abundance of zooplankton and of benthic invertebrates.

METHODS

In 1998, samples were taken from all five lakes aboard the R/V *Lake Guardian* during both a spring and a summer cruise, running from 29 March to 14 May, and 2 August to 5 September, respectively. Between 8 and 20 stations were sampled on each lake for plankton (Fig. 1). Stations were originally selected to represent specific open lake areas which had been identified as homogeneous by earlier surveys, with nearshore areas explicitly excluded (Rockwell *et al.* 1989). Within each of these homo-

geneous areas the station located at the deepest sounding is designated a master station, at which additional samples are taken in the upper fifty meters. There are two or three such stations in each lake.

At each station, water column profiles for temperature, conductivity, turbidity, pH, and *in vivo* chlorophyll fluorescence were taken using a Seabird STE-911 CTD multi-sensor unit. Integrated samples for nutrients, *in vitro* chlorophyll *a*, and phytoplankton enumeration were created from a composite of water samples taken at discrete depths (Spring: surface, 5 m, 10 m, and 20 m; Summer: surface, 5 m, 10 m, and lower epilimnion) with Niskin bottles mounted on a SeaBird Carousel Water Sampler. Samples for total soluble phosphorus (TSP) were filtered in the field through 0.45 μm SartoriusTM filters and preserved with H_2SO_4 for later analysis in the lab. Samples for soluble silica (Si) were stored at 4°C. Samples for phytoplankton analysis were preserved in the field with Lugol's solution, and with formalin upon return to the laboratory.

After acid persulfate digestion, TSP was measured on a Lachat QuikChem AE autoanalyzer by the ascorbic acid method (APHA 1985). Si was determined by the molybdate method on a Lachat QuikChem AE autoanalyzer (APHA 1985). Chlorophyll *a*, uncorrected for pheophytin, was determined on a Turner Designs 10-AU fluorometer following the method of Welschmeyer (1994).

Phytoplankton abundances were estimated, and *Urosolenia* (= *Rhizosolenia*) species and all non-diatom phytoplankton were identified, using the Utermöhl technique (Lund *et al.* 1958) at a magnification of 500x, with diatoms other than *Urosolenia* identified as either centrics or pennates. At least 250 individuals were enumerated along parallel transects across the middle of the chamber. Diatoms were identified (500 frustules), and relative abundances determined, separately on permanent slide mounts of digested material at 1,250x. Relative proportions of each taxon of centrics and pennates were multiplied by the appropriate Utermöhl counts to determine abundances. It has been pointed out that techniques other than the Utermöhl technique are inadequate for the identification of small flagellates (Munawar and Munawar 1975), while the Utermöhl technique hinders proper species identification of diatom taxa (Wolin *et al.* 1991). Primary taxonomic keys used were Prescott (1962), Krammer and Lange-Bertalot (1991, 1997), Patrick and Reimer (1966, 1975), Germain (1981), Huber-

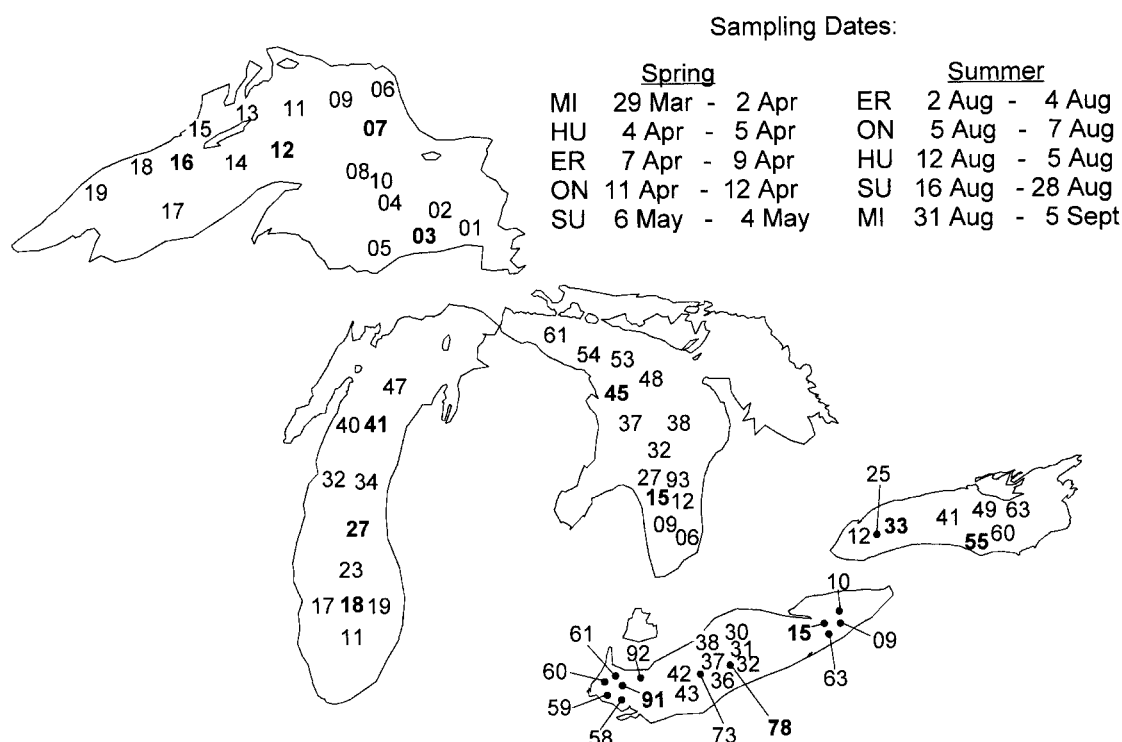


FIG. 1. Locations of plankton sampling stations and sampling dates during the 1998 GLNPO survey. Master stations are shown in bold.

Pestalozzi (1941, 1968, 1983), and Drouet and Daily (1973). At least 10 individuals of each taxon were measured per sample, and cell volumes computed using appropriate geometrical formulae. To increase comparability with previous studies, phytoplankton biomass is reported as gm/m^3 , assuming a specific gravity of 1.

Patterns in phytoplankton community composition across the lakes were explored with the use of detrended correspondence analysis, using the program CANOCO v 4.0. Prior to analysis, biomass was converted to natural logarithms to reduce the undue influence of a few dominant species, and rare species (no more than 5% of any sample) were excluded from analysis to reduce noise (Gauch 1982). To help identify the environmental gradients associated with the ordination axes, correlations were calculated between environmental variables and axis scores for each sample, and the resulting correlation coefficients were plotted against axis scores. The relationship between environmental variables and ordination axes were represented in ordination space as lines, with the angle of the line indicating the degree of correlation with the two axes, and the length of the line indicating the strength of that cor-

relation. The relationship between environmental variables and the DCA results was further examined by plotting the ordination results with individual points sized according to the variables which appeared to have the most effect.

RESULTS

General Limnological Conditions

Temperatures across the lakes during the spring cruise were between 2 and 4°C, with the exception of the shallow western basin of Lake Erie, where temperatures reached 7.6°C (Fig. 2). Concentrations of most chemical constituents showed a general trend of increase from upstream to downstream, i.e., along the sequence Superior, Michigan, Huron, Erie, and Ontario. Lake Michigan was often an exception to this sequence, however, exhibiting relatively elevated levels of alkalinity, chloride, pH, and conductivity. In the case of both chlorophyll and dissolved phosphorus, Lake Erie exhibited the highest average concentrations. Dissolved silica showed a reverse trend, generally decreasing from upstream to downstream. Nitrate showed very little variation across the lakes.

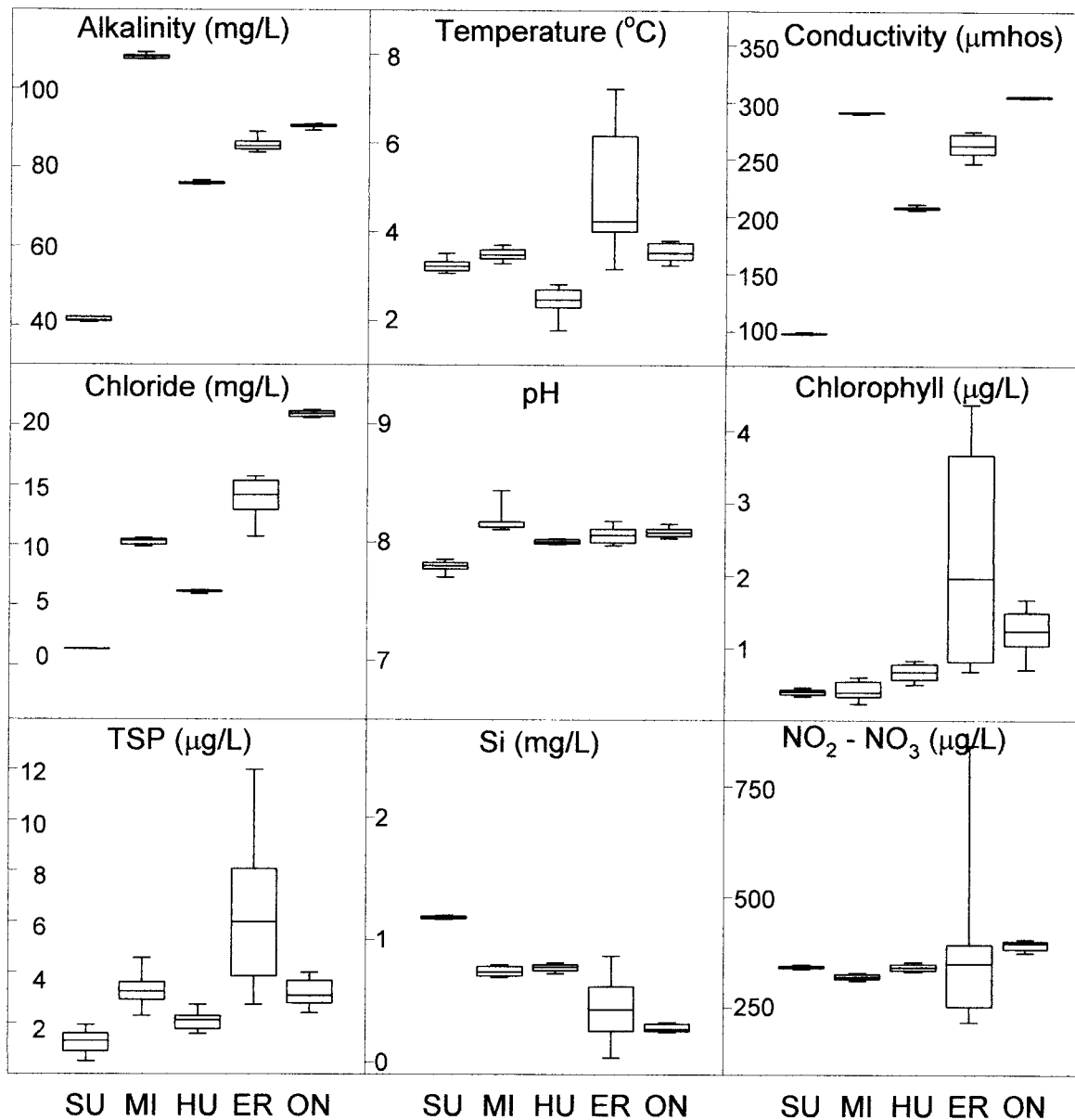


FIG. 2. Box plots of selected physical and chemical variables for the Great Lakes, spring 1998. Boxes represent 25th, 50th, and 75th percentiles; whiskers indicate 10th and 90th percentiles.

During the summer cruise, stable stratification had developed at nearly all open water sites in all lakes except for Lake Erie, where stratification was only evident in the deeper eastern basin. The depth of the epilimnion (delimited by a greater than 1°C difference per meter) ranged from 5.5 m in western Ontario to 23.5 m in northern Lake Superior, averaging between 14 and 17 m for the upper lakes and 19 and 11 m for Lakes Erie and Ontario, respec-

tively. Epilimnetic temperatures at most sites were generally between 21 and 24°C, with the exception of Lake Superior, where temperatures were only about 10°C (Fig. 3).

During the summer, pH values across the lakes were higher than in the spring, and differences between the lakes were somewhat more pronounced. As in the spring, pH in Lake Superior was substantially lower than the other lakes, and Lakes Michi-

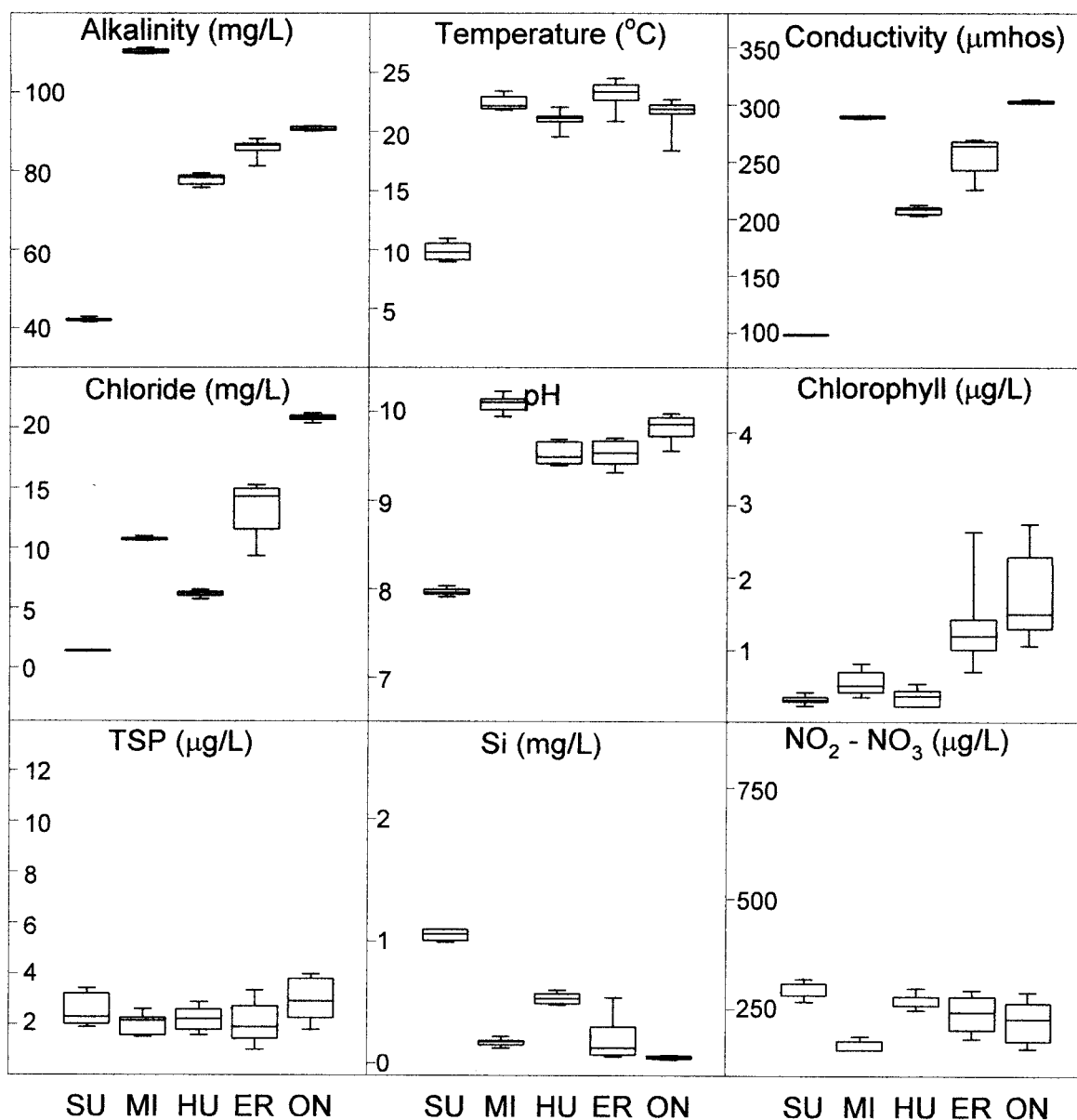


FIG. 3. Box plots of selected physical and chemical variables for the Great Lakes, summer 1998. Boxes as in Figure 2.

gan and Ontario somewhat higher. Values for chloride, alkalinity, and conductivity were essentially identical to those in the spring. Both total soluble phosphorus and chlorophyll were substantially higher in the lower lakes compared to the upper lakes, with Lake Ontario on average exhibiting the highest values for both parameters. Available nitrogen fluctuated within a very narrow range for all lakes, while dissolved silica was highest in Lake Superior and Lake Huron.

Phytoplankton

Spring

Total phytoplankton biomass across the lakes in the spring varied by over two orders of magnitude, ranging between about 0.026 gm/m³ at a site in Lake Superior to 6.0 gm/m³ at a site in Lake Erie (Fig. 4). A particularly high degree of spatial heterogeneity was seen in Lake Erie, where biomass varied by more than a factor of 40. This heterogene-

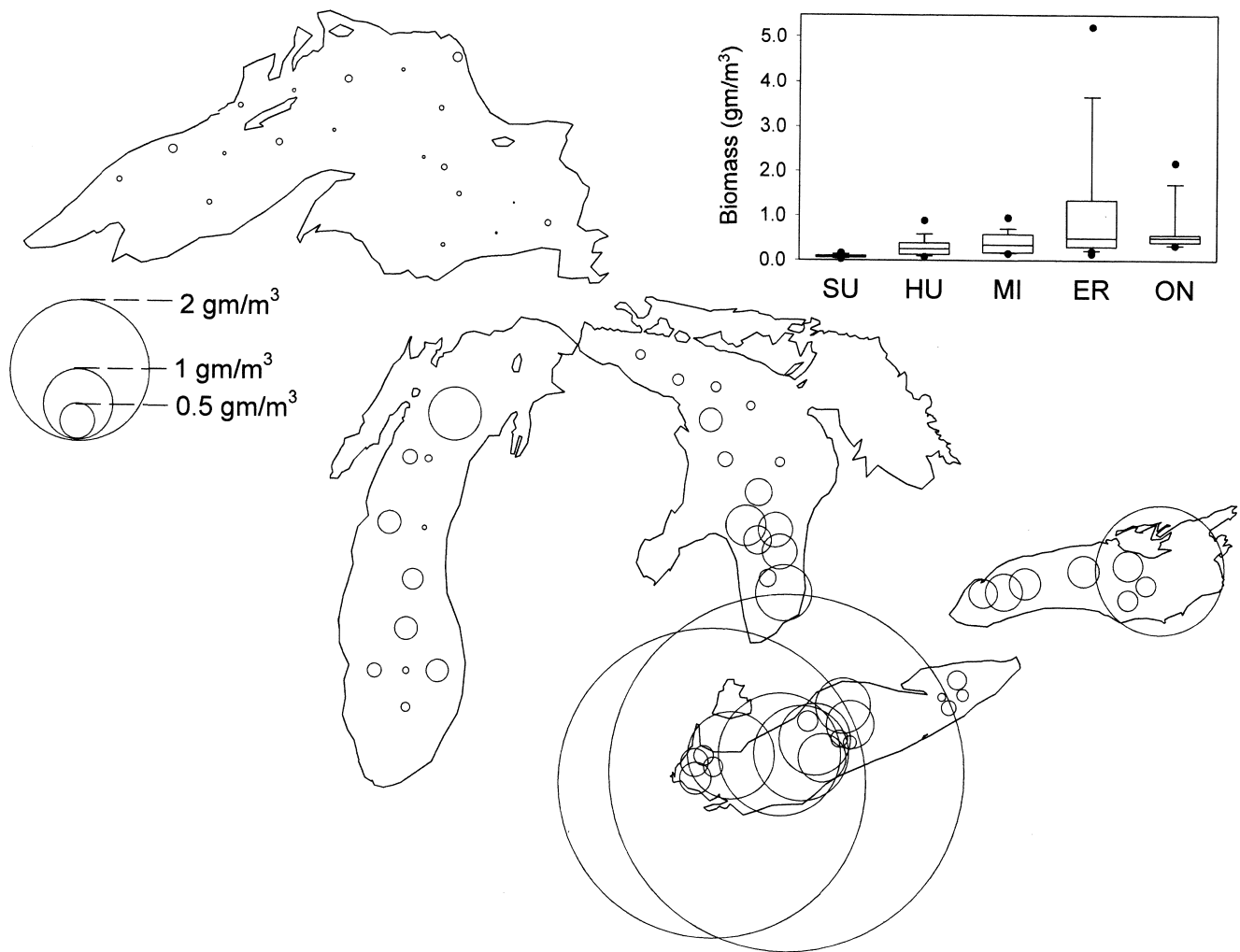


FIG. 4. Biomass of the total phytoplankton community in the Great Lakes, spring 1998. Inset shows box plots of phytoplankton biomass for each lake. Boxes represent 25th, 50th, and 75th percentiles; whiskers indicate 10th and 90th percentiles, points indicate outliers.

ity was not confined to between-basin differences; while biomass was uniformly low in the eastern basin of Lake Erie, a high degree of variability was seen within both the central and western basins. There were also some differences in biomass in Lake Huron, where biomass values in the southern part of the lake were on average higher than those in the northern part of the lake. Median biomass for each lake, however, was relatively similar, ranging only from 0.26 gm/m³ in Lake Michigan to 0.52 gm/m³ in Lakes Erie and Ontario. The exception was Lake Superior, whose median biomass was substantially lower than the other lakes (0.085 gm/m³).

During spring, 261 phytoplankton taxa were

identified in the 72 samples examined. All lakes supported over one hundred taxa, with Lakes Superior and Huron having the greatest number (Fig. 5). Average numbers of taxa per site for the lakes ranged from 42 in Lake Erie to 73 in Lake Huron. Diatoms were overwhelmingly the most diverse group across all lakes, contributing between 52 and 74 taxa per lake. Chlorophytes and chrysophytes each contributed between about 20 and 40 taxa per lake, while between 10 and 12 cryptophyte taxa were found in each lake. Other groups, while occasionally responsible for high numbers of individuals, were considerably less diverse.

Diatoms contributed the majority of biovolume at most sites, with the lake-wide median percent con-

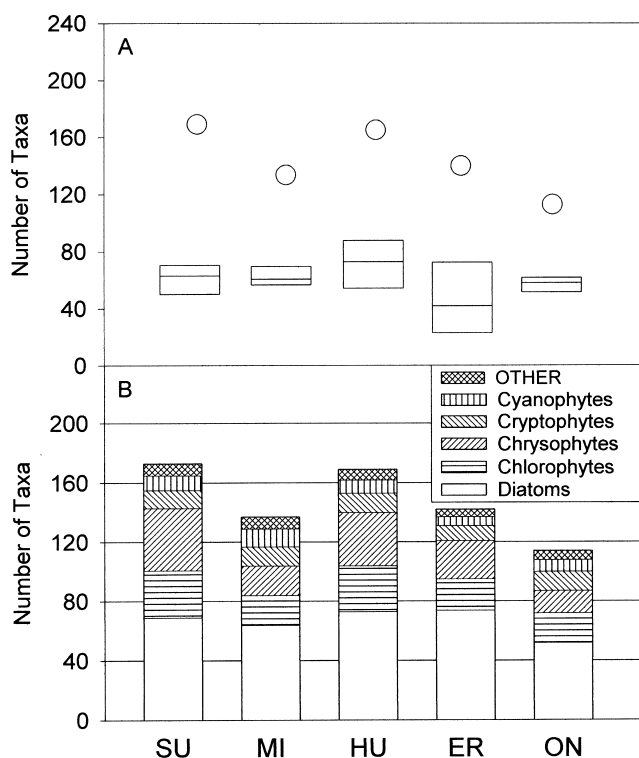


FIG. 5. A.) Numbers of phytoplankton taxa identified per lake during spring cruise, 1998. Boxes represent minimum, mean, and maximum numbers of taxa per station for each lake; circles represent total numbers of taxa found in each lake; B.) Contribution of major taxonomic groups to numbers of taxa.

tribution of diatoms to total phytoplankton biovolume between about 70 and 80%, although Lake Superior was substantially lower (33%; Fig. 6). The majority of this, in turn, was comprised of centric diatoms. Cryptophytes were the second most important group in most lakes, in terms of biovolume, contributing between 6% (Lake Erie) and 27% (Lake Superior) of phytoplankton biovolume. Cyanophytes were a relatively minor component of the communities at most sites, although substantial populations were found at some sites in Lake Superior and in southern Lake Huron. Biovolumes of chlorophytes were uniformly low throughout the lakes in spring.

All lakes supported large populations of the filamentous centric diatom *Aulacoseira islandica* (O.Müll.) Simonsen. When species biovolumes were averaged across lakes, *A. islandica* was the

dominant species in all lakes except Superior, where its biomass was exceeded only by *Rhodomonas minuta* Skuja (Table 1). In Lakes Erie, Huron, and Ontario, *A. islandica* biovolume was at least three times larger than that of the next dominant species. While *A. islandica* was found at virtually all stations in the spring, its congener *Aulacoseira subarctica* (O.Müll.) Haworth was confined to Lakes Michigan, Huron, and, in limited numbers, some sites in the central and western basins of Lake Erie.

Members of the genus *Stephanodiscus* were among the ten most dominant species in all lakes, and included *Stephanodiscus parvus* Stoerm. & Hak., *S. hantzschii* fo. *tenuis* Hak. & Stoerm. (= *Stephanodiscus tenuis* Hust.), and *Stephanodiscus binderanus* (Kütz.) Krieg.. It is noteworthy that *Stephanodiscus hantzschii* Grun. and *S. hantzschii* fo. *tenuis*, which are considered to be different forms of the same species (Håkansson and Stoermer 1984), showed very little overlap in their ranges, the latter most prevalent in the central and eastern basins of Lake Erie and the former occurring in the western basin of Lake Erie and throughout Lake Ontario. Although *S. binderanus* was largely confined to a few sites in central Lake Erie, populations there were extremely large. Most sites supported substantial populations of *Cyclotella comensis* Grun. and/or *Cyclotella ocellata* Pant., with exceptions being Lake Ontario and the eastern basin of Lake Erie. These two species, along with *Cyclotella pseudostelligera* Hust., made up a significant portion of the overall diatom community at most sites in Lake Superior. Species of *Urosolenia* (*Urosolenia eriensis* (H.L.Sm.) Round & Crawford, *Urosolenia longiseta* (Zach.) Edlund & Stoerm., and *Urosolenia* spp.) were also distributed at most sites, again with the exception of Lake Ontario and the eastern and most of the central basin of Lake Erie.

Two non-indigenous centric diatoms were also found in the lakes, apparently for the first time. *Thalassiosira baltica* (Grun.) Ostensfeld, a species previously reported from the sediments of Lake Ontario and thought to be an introduction (Edlund *et al.* 2000), was found throughout Lake Ontario and, in limited numbers, in eastern Lake Superior. An organism identified as *Stephanocostis* Genkal & Kosmina, first described from Siberia (Genkal and Kuzmina 1985), was found in small numbers at a limited number of sites in Lake Superior.

Only two pennates appeared in significant numbers in the spring: *Asterionella formosa* Hass. and

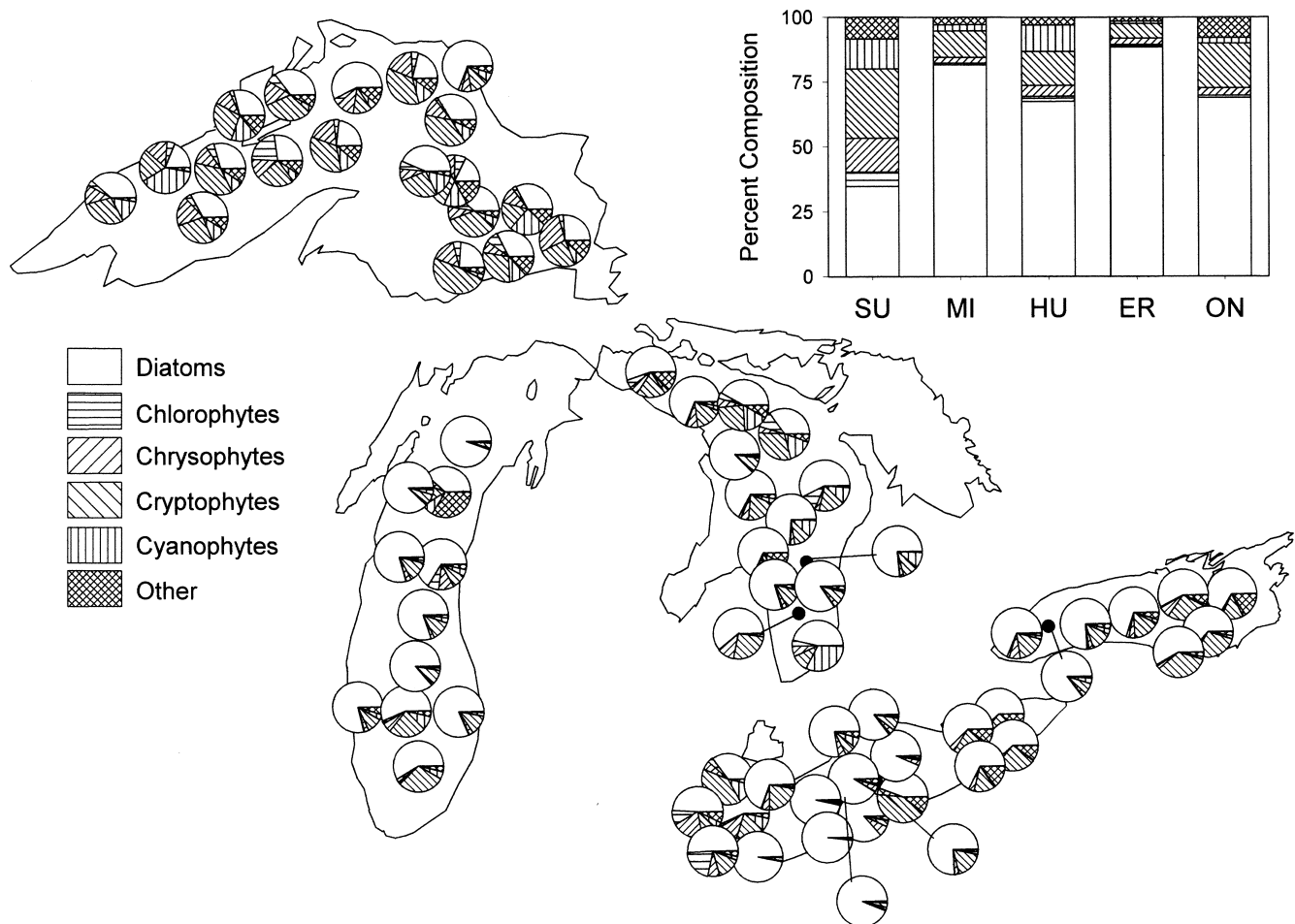


FIG. 6. Relative biomass of major phytoplankton groups in the Great Lakes, spring 1998. Inset shows whole-lake averages.

Synedra filiformis Grun. Both organisms were widely distributed in the lakes, with the exception of the eastern and central basins of Lake Erie.

Of the non-diatoms, cryptophytes appeared in substantial populations in all lakes, usually represented by members of the genus *Rhodomonas*. The cyanophyte genus *Oscillatoria* attained large populations at some sites in Lake Huron, and as a result was the second most dominant species across the whole lake, while the small colonial coccoid cyanophyte *Anacystis montana* fo. *minor* Dr. & Daily appeared in appreciable numbers in Lakes Erie and Superior. Several species of *Gymnodinium* contributed a moderate amount of biomass in Lakes Michigan, Ontario, and Superior. Populations of chlorophytes and chrysophytes were uniformly small in the spring.

Detrended correspondence analysis of spring data resulted in separation of all of the lakes except for Lakes Michigan and Huron, which were largely indistinguishable by the technique (Fig. 7). Most of the variation captured by the first ordination axis was contributed by Lake Erie, which was spread out along this axis with the western basin close to the upper lakes. Sites from the other four lakes occupied an extreme position with respect to axis one, and were largely separated from each other by axis two. Interestingly, the sequence along axis two was Michigan/Huron, Superior and Ontario, suggesting a closer affinity between communities in Lakes Superior and Ontario than between those in Lakes Michigan/Huron and Ontario.

When environmental variables were correlated with ordination axis scores, particularly strong cor-

TABLE 1. Average lakewide biomass ($\mu\text{g/mL}$) of dominant (> 5% biomass at any site) phytoplankton taxa, spring, 1998. Numbered taxa have been described in-house.

	Superior	Michigan	Huron	Erie	Ontario
BACILLARIOPHYTA					
<i>Asterionella formosa</i> Hass.	1,904	641	4,207	4,875	3,420
<i>Aulacoseira islandica</i> (O. Müll.) Simonsen	8,669	86,441	149,213	786,555	242,768
<i>Aulacoseira subarctica</i> (O. Müll.) Haworth	298	73,867	34,486	5,063	238
<i>Cyclotella comensis</i> Grun.	377	276	603	6,583	244
<i>Cyclotella comta</i> (Ehr.) Kütz.	4,739	1,197	2,832	224	187
<i>Cyclotella ocellata</i> Pant.	1,689	2,277	1,096	3,714	10
<i>Nitzschia lauenburgiana</i> Hust.	79	760	484	658	9,062
<i>Urosolenia</i> spp.	490	654	2,160	1,486	152
<i>Stephanodiscus alpinus</i> Hust.*	1,059	17,273	2,621	22,608	154,957
<i>Stephanodiscus binderanus</i> (Kütz.) Krieg.	0	0	0	32,028	1,183
<i>Stephanodiscus hantzschii</i> f. <i>tenuis</i> Hak. & Stoerm.	2	44	45	70,265	363
<i>Stephanodiscus niagarae</i> Ehr.	2,488	0	3,817	56,404	0
<i>Stephanodiscus parvus</i> Stoerm. & Hak.	14	1,032	728	17,672	265
<i>Stephanodiscus subtransylvanicus</i> Gasse	3,007	59,003	5,775	505	0
<i>Tabellaria fenestrata</i> (Lyngb.) Kütz.	0	0	7,797	0	0
<i>Tabellaria flocculosa</i> (Roth) Knud.	1,688	919	28,456	3,597	7,144
<i>Thalassiosira baltica</i> (Grunow) Ostensfeld	90	0	0	0	41,246
<i>Thalassiosira weissflogii</i> (Grun.) G. Fryx. & Hasle	0	14	0	2,798	0
CHLOROPHYTA					
<i>Closterium gracile</i> Breb.	0	0	1,033	0	0
<i>Closterium parvulum</i> Nag.	0	0	859	0	0
Cocoid oval	235	45	101	1,841	60
<i>Cosmarium</i> spp.	1,086	0	0	0	781
<i>Oocystis borgei</i> Snow	216	0	39	0	0
<i>Pediastrum boryanum</i> (Turp.) Menegh.	0	0	0	5,782	0
CHRYSOPHYTA					
<i>Dinobryon cylindricum</i> Imhof	755	62	81	0	0
Haptophyceae	4,537	1,477	7,448	7,106	9,056
<i>Mallomonas</i> spp.	1,016	1,332	1,382	0	0
<i>Ochromonas</i> spp.—ovoid	1,505	1,117	1,957	4,069	2,872
<i>Stelemonas dichotoma</i> Lack.	74	185	105	8,266	0
CRYPTOPHYTA					
<i>Cryptomonas erosa</i> Ehr.	4,661	9,056	4,878	0	19,535
<i>Cryptomonas erosa</i> var. <i>reflexa</i> Marss.	1,108	2,525	4,052	740	6,669
<i>Cryptomonas marssonii</i> Skuja	883	283	858	951	4,055
<i>Cryptomonas ovata</i> Ehr.	853	5,854	2,655	0	11,597
<i>Cryptomonas phaseolus</i> Skuja	1,694	1,840	4,176	1,130	4,492
<i>Cryptomonas pyrenoidifera</i> Geitl.	1,244	289	4,902	1,479	3,967
<i>Rhodomonas lens</i> Pasch. & Rutt.	892	5,403	8,027	5,627	6,019
<i>Rhodomonas minuta</i> Skuja	9,327	3,564	16,133	40,481	43,431
<i>Rhodomonas minuta</i> var. <i>nannoplanctica</i> Skuja	1,010	1,223	2,179	14,304	4,960
CYANOPHYTA					
<i>Anacystis montana</i> fo. <i>minor</i> Dr. & Daily	3,750	2,939	2,644	10,718	6,206
<i>Microcystis aeruginosa</i> (Kütz.) emend. Elenkin	610	92	0	0	0
<i>Oscillatoria minima</i> Gick.	3,709	392	573	0	3,974
<i>Oscillatoria tenuis</i> C.A. Ag.	0	0	35,682	0	0
PHYRROPHYTA					
<i>Gymnodinium helveticum</i> fo. <i>achroum</i> Skuja	0	3,527	4,279	0	38,579
<i>Gymnodinium</i> spp.	3,977	3,343	3,613	2,037	12,517
UNIDENTIFIED					
Unidentified cocoid ovoid (Chrysophyta)	1,490	1,253	1,436	2,092	1,933
Unidentified flagellate #5	5	18	28	9,779	792
Unidentified flagellate ovoid	1,149	203	1,250	4,203	3,075

* Probably includes one or several as-yet unrecognized '*S. alpinus*-like' taxa.

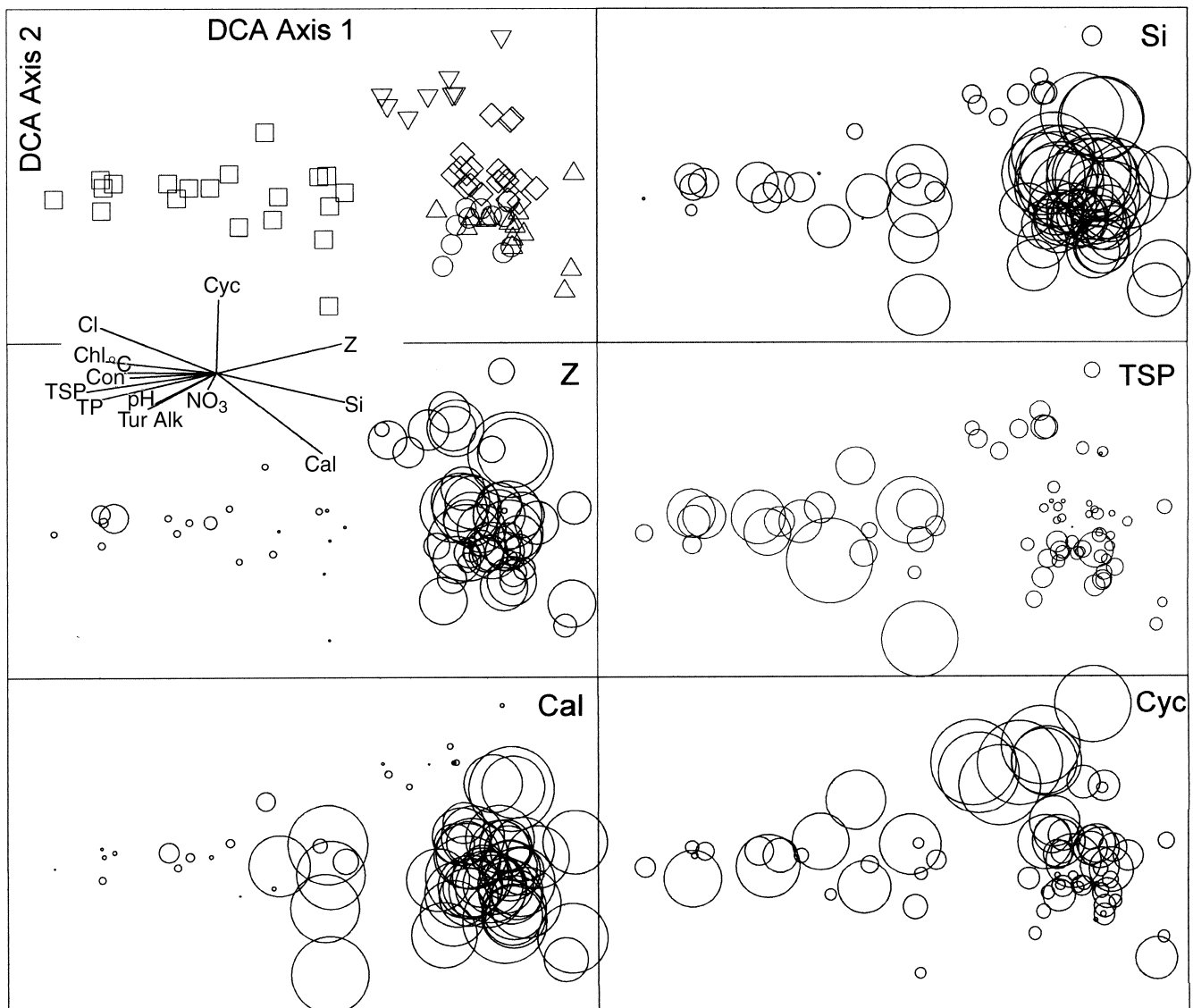


FIG. 7. Results of detrended correspondence analysis (DCA) of spring 1998 phytoplankton data (\diamond = Superior; \circ = Michigan; \triangle = Huron; \square = Erie; ∇ = Ontario), and DCA results with site scores sized according to selected environmental variables (abbreviations as below). Inset shows correlations of environmental variables with ordination axis scores. The angle of the line indicates the degree of correlation with the two axes, and the length of the line indicates the strength of that correlation. Cl = chloride; Chl = chlorophyll *a*; $^{\circ}\text{C}$ = temperature; TSP = total soluble phosphorus; TP = total phosphorus; Z = depth; Si = dissolved silica; Con = conductivity; Alk = alkalinity; Tur = turbidity; NO_3 = nitrate and nitrite; Cal = percent of crustacean community comprised of calanoid copepods; Cyc = percent of crustacean community comprised of cyclopoid copepods.

relations were found with zooplankton community composition, depth, nutrients, chloride, and chlorophyll *a* (Fig. 7). The main separation of sites, roughly along a gradient parallel to axis one, was most strongly associated with differences in silica concentration, depth, and total soluble phosphorus.

While depth and total soluble phosphorus appeared to have the primary effect of separating Lake Erie from the other lakes, a broad gradient of silica appeared to contribute to the separation of the upper lakes and the western basin of Erie from the rest of Lake Erie and Lake Ontario. There were also strong

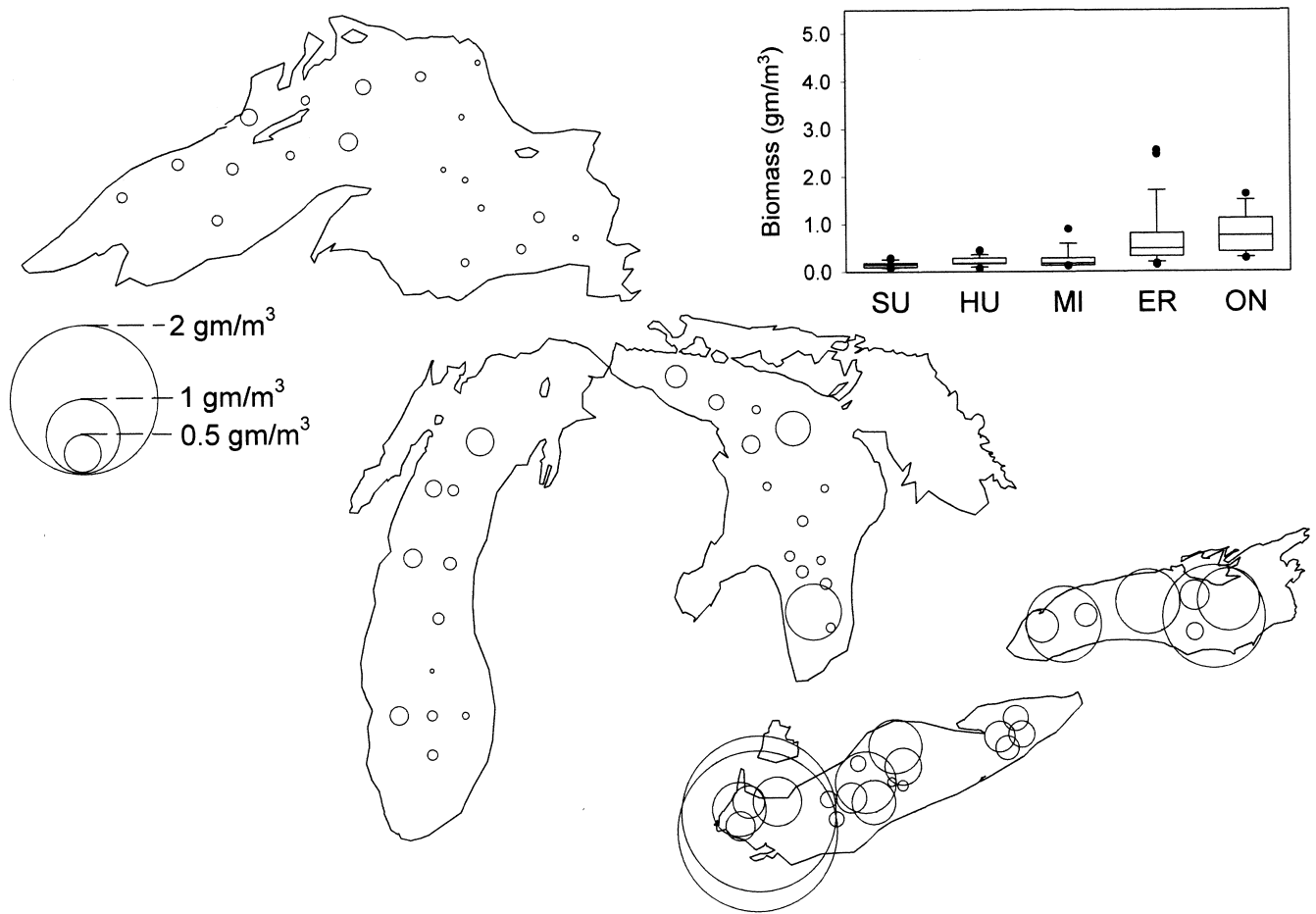


FIG. 8. Biomass of the total phytoplankton community in the Great Lakes, spring 1998. Inset shows box plots of phytoplankton biomass for each lake; boxes as in Figure 4.

associations between zooplankton community composition and the positions of phytoplankton communities in ordination space. Percent contribution of calanoid copepods to total crustacean biomass was equally strongly correlated with both ordination axes, and appeared to contribute to the separation of Lake Ontario and some sites in Lake Erie at the upper left fringe of the ordination from all other sites. Percent contribution of cyclopoid copepods was correlated almost entirely with axis one, and was therefore most responsible for the sequence of lakes along this axis.

Summer

Total biomass at sites across the lakes in the summer were confined to a narrower range compared to spring, varying from 0.07 gm/m³ at a site in Lake

Michigan to 2.54 gm/m³ at a site in Lake Erie (Fig. 8). Lake-wide median biomass was also more similar in summer compared to spring, due mostly to larger biomass in Lake Superior. As in the spring, though, a high degree of spatial heterogeneity in phytoplankton biomass was seen in Lake Erie, and as in spring, this variability was seen within basins, particularly the central basin.

A total of 285 phytoplankton taxa were identified from epilimnetic samples taken during the summer cruise, a number similar to that found in the spring. Numbers of taxa found at each lake, and numbers of taxa found at sites within lakes, were also similar to those in the spring, although Lake Erie had slightly greater species richness in the summer compared to the spring (Fig. 9). The contribution of different phytoplankton divisions to species diversity was similar to that of spring, although diatoms

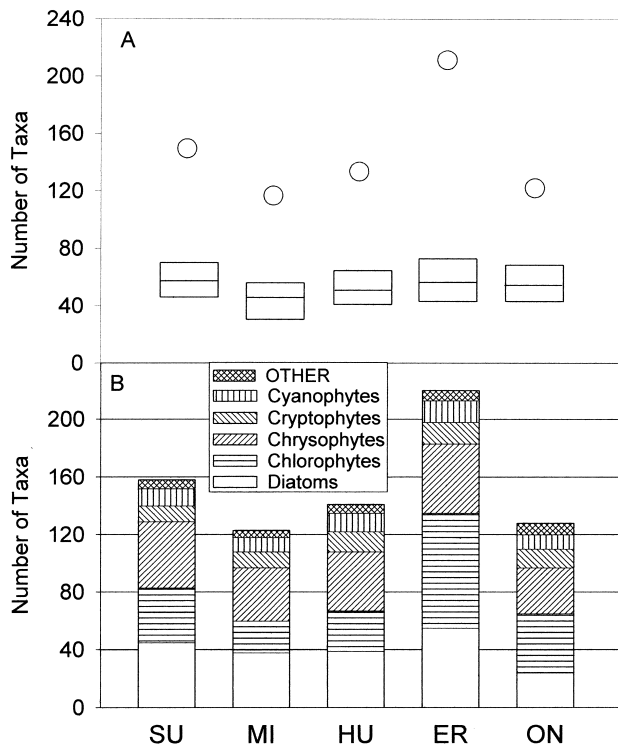


FIG. 9. A.) Numbers of phytoplankton taxa identified per lake during summer cruise, 1998. Boxes represent minimum, mean, and maximum numbers of taxa per station for each lake; circles represent total numbers of taxa found in each lake; B.) Contribution of major taxonomic groups to taxa richness.

contributed somewhat less species and chlorophytes and chrysophytes slightly more. Again, the contribution of cryptophytes and cyanophytes to species richness was 10% or less.

Summer phytoplankton communities exhibited a shift away from diatoms, with proportions of chrysophytes increasing dramatically in the upper lakes, and proportions of chlorophytes increasing substantially in Lakes Erie and Ontario (Fig. 10). Biomass of cyanophytes showed notable increases in Lakes Erie and Michigan. In Lakes Michigan and Huron, the colonial *Chrysosphaerella* was the dominant chrysophyte, while all three upper lakes supported large populations of the genus *Dinobryon*, particularly Lake Superior where this genus contributed four of the ten most dominant species (Table 2). While chlorophytes increased in both lower lakes, the dominant species differed. In Lake Erie, the

chlorophyte *Pediastrum* contributed a large amount of biomass at sites throughout the western and central basin, but did not show up in substantial amounts elsewhere. Chlorophytes in Lake Ontario were predominantly members of the genera *Staurastrum*, *Oocystis*, *Tetraedron*, and *Scenedesmus*. Dinoflagellate biomass also increased in all lakes, except Superior, with several sites in Lake Ontario apparently supporting particularly large amounts. However, these were often the result of single large individuals of *Ceratium hirundinella* (O.Müll.) Dujardin or *Peridinium* showing up in counts, so estimates of biomass of this division should be interpreted with caution. The cryptophytes *R. minuta* and/or *Cryptomonas erosa* Ehr. were among the dominant species in all lakes. This pattern was consistent during the spring and summer.

Summer diatom communities were substantially less diverse than in spring. Dominants across all lakes were drawn from a limited pool of species, including members of the genus *Cyclotella*, *Synedra filiformis* Grun., *Fragilaria crotonensis* Kitt. and several *Urosolenia* species. Some broad difference in species composition were noted, however. Lake Superior had the richest *Cyclotella* flora, numerically dominated by *Cyclotella delicatula* Hust. and an extremely small (diameter ~ 4 µm) taxon tentatively identified as *C. pseudostelligera*, but containing 16 taxa in all (Table 3). In Lake Ontario, on the other hand, *Cyclotella* populations were both the smallest in the lakes, both in terms of absolute numbers and proportion of the phytoplankton, and had the fewest number of taxa, with over 75% of the taxa comprised of *C. comensis*. Numbers of *Cyclotella* taxa and their relative proportions were similar in Lakes Huron and Michigan, with *C. comensis*, a small (~5 µm), apparently related form designated *C. comensis* var. #1, *C. delicatula* Hust. and *C. pseudostelligera* most prominent. Some differences were noted in the distribution of *Cyclotella* species between the different basins of Lake Erie, most notably the diminishing relative importance of *C. ocellata* from west to east, and the relative lack of *C. comensis* var. #1 in the western basin. Populations of *Cyclotella* were substantially higher in the central basin in comparison to both the other two basins, and the other lakes. *S. filiformis*, which was widely distributed throughout most of the lakes, was relatively uncommon in Lake Superior, and was represented mostly by its variety *Synedra filiformis* var. *exilis* A.Cleve. in Lake Ontario. Species

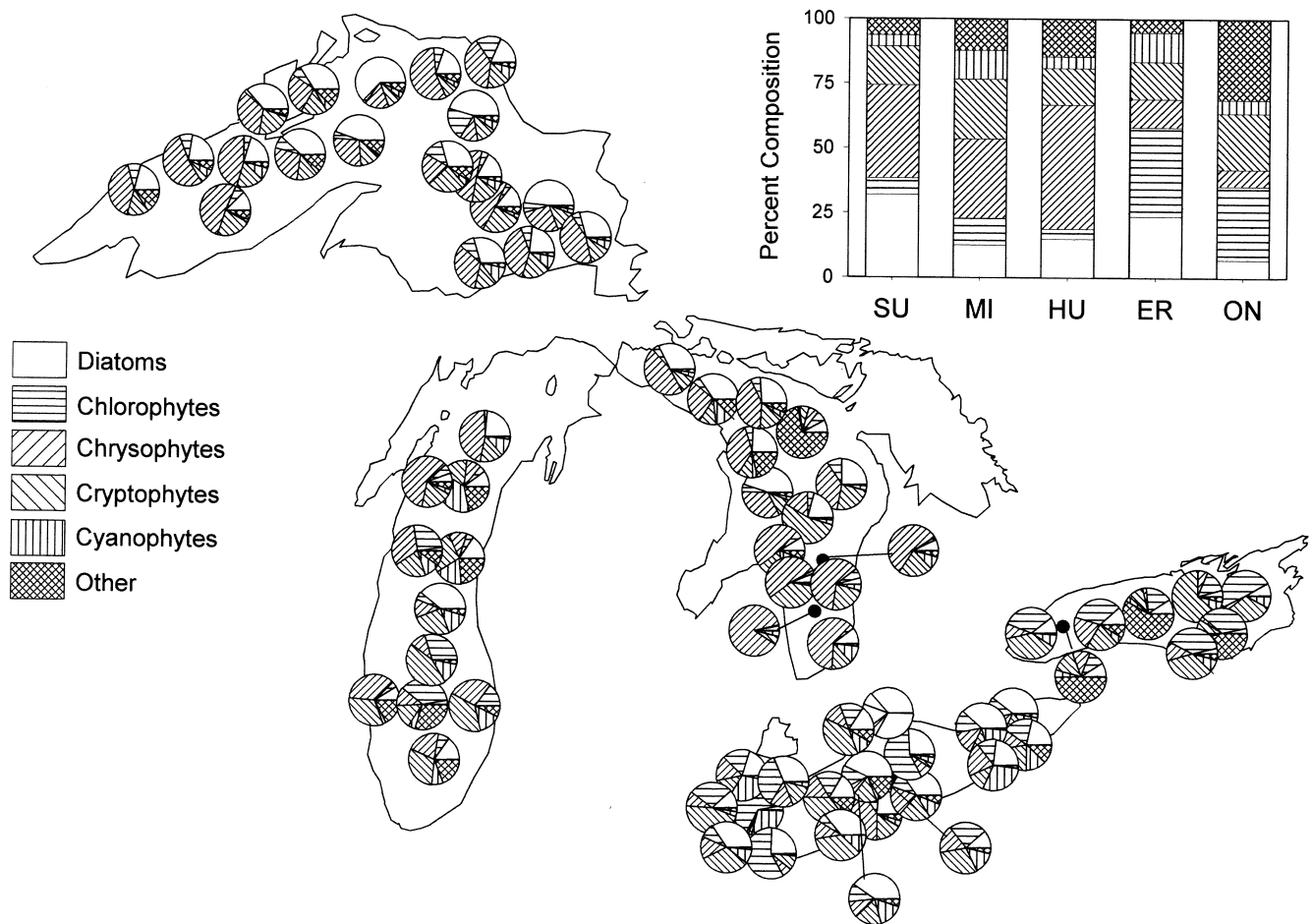


FIG. 10. Relative biomass of major phytoplankton groups in the Great Lakes, spring 1998. Inset shows whole-lake averages.

of *Urosolenia* appeared in all lakes in significant numbers except Lake Ontario, but were most common in Lake Superior, where the species *U. longiseta* was found at nearly every site.

Ordination analysis of phytoplankton community data in summer resulted in considerably less clear separation of the lakes than in the spring (Figure 11), with the striking exception of Lake Ontario, which was entirely separated from the other lakes. Correlations with environmental factors indicated a broad trophic gradient, with most nutrients and chlorophyll *a* increasing from the upper left to the lower right of the ordination diagram, and silica displaying the opposite trend, although when these variables were examined individually clear patterns were not always discernible (Fig. 11). The two variables exhibiting the most obvious relationship to the ordination in the summer were chlorophyll *a*

and silica, the latter of which appeared to be most responsible for the extreme position of Lake Ontario in the ordination diagram. In contrast to the spring, zooplankton community composition showed no discernible patterns with the positions of sites in ordinations space, in spite of the relatively high correlation coefficients between both cyclopoid copepod and bosminid cladoceran dominance and the ordination axes.

DISCUSSION

Species Richness

These results have corroborated the fact that the phytoplankton communities in the Great Lakes are extremely diverse. In the course of this study between 180 (Lake Michigan) and 288 (Lake Erie) taxa were identified in the lakes. Other studies have

likewise found that the lakes support high numbers of species. Munawar and Munawar (1978) identified 285 species from Lake Superior in 1973; Makarewicz and Bertram (1991) reported between 210 and 333 species from three years of Lake Huron data; Makarewicz (1993) reported between 286 and 346 taxa in five years of Lake Erie data, while Munawar *et al.* (1974) and Gray (1987) found 100 and 174 species in Lake Ontario, respectively. Overall, about half of the species found during this study were diatoms, with chlorophytes contributing about half as many species (25%) and chrysophytes half again (13%). These proportions are very similar to those reported in previous years from the program (Makarewicz and Bertram 1991, Makarewicz 1993), though workers outside the program have found a lesser contribution to species richness from diatoms (Lake Ontario: 25%, Munawar *et al.* 1974, western basin Lake Erie: 18%, Gladish and Munawar 1980). This difference is probably due to the fact that diatoms are identified separately, after digestion, in this program, rather than included in Utermöhl counts, which would undoubtedly lead to a greater number of species being successfully identified.

Patterns of species richness among the major taxonomic groups were surprisingly similar from lake to lake, in spite of differences in the contributions of these groups to total biomass. Diatoms contributed more species than other groups in the spring, between about 40 and 50%, with chrysophytes usually second in species richness, even though they contributed very slightly to the biomass in most lakes at this time. In the summer, chlorophytes and chrysophytes were among the most taxa rich groups across all lakes, in spite of the former contributing little biomass to the upper lakes, and the latter contributing little to the lower lakes.

Community Composition

Lake Superior was distinguished from other lakes in this study both by the sparsity of the phytoplankton community, and by the relatively low abundance of diatoms in the spring, during which time all other lakes were overwhelmingly dominated by diatoms. Because of its size and remoteness, Lake Superior is probably the least studied of the Laurentian Great Lakes, particularly with respect to open water communities. Consequently, very few comparative data exist for the phytoplankton community in the lake. The earliest reports indicated that the lake was dominated by diatoms, with the

genera *Fragilaria*, *Asterionella*, *Tabellaria*, *Melosira* (= *Aulacoseira*), and *Urosolenia* mentioned specifically. Several studies also reported *Dinobryon* to be common, or even dominant (Davis 1966). More recent studies have found dominance by *Cyclotella* in the summer (Holland 1965, Schelske *et al.* 1972), a genus that was co-dominant with *Dinobryon* during August of this study. Fahnenstiel and Glime (1983) found phytoflagellates, notably *R. minuta*, *Cryptomonas* spp., and *Ochromonas* spp., dominating during spring, and being replaced by *Cyclotella* after stratification. These results are supported by those of this study, which showed a lake dominated by various cryptophytes, *Aulacoseira islandica* and members of the genera *Dinobryon* and *Cyclotella*, with the latter two more prevalent in the summer, and suggest that the lake has changed little in the past twenty years. Unlike Munawar and Munawar (1975), though, who reported little seasonality in the phytoplankton community in 1973, a distinct seasonal difference in community composition was identified in this study, with the spring form *A. islandica* largely disappearing in the summer, and populations of both *Dinobryon* and *Cyclotella*, as well as overall biomass, increasing at that time.

Most historical reports of Lake Michigan phytoplankton indicate that it was dominated by diatoms at all times, with dominant genera listed as *Synedra*, *Fragilaria*, *Tabellaria* and *Asterionella*, as well as the chrysophyte *Dinobryon* (Davis 1966). Studies of the extreme southern basin in the early 1960s corroborate the importance of diatoms throughout the year (Stoermer and Kopczynska 1967).

Lake Michigan has been shown to have undergone a dramatic decrease in dissolved silica concentrations from the mid 1950s through 1970 (Schelske 1988), which resulted from increased phosphorus loading during that time and consequent increased deposition of silica to the sediments through increased diatom production (Schelske and Stoermer 1971). These changed nutrient conditions are thought to have promoted increases in the dominance of chlorophytes and cyanophytes during the late 1960s and 1970s (Fahnenstiel and Scavia 1987). For example, in mid-August 1976, about 75% of the phytoplankton biomass at northern open water stations was comprised of approximately equal proportions of cyanophytes, chlorophytes, and cryptophytes, with diatoms contributing only about 20% to overall biomass (Bartone and Schelske 1982). Similarly, Chang and Rossmann

TABLE 2. Average lakewide biomass ($\mu\text{g/mL}$) of dominant (> 5% biomass at any site) phytoplankton taxa, summer, 1998.

	Superior	Michigan	Huron	Erie	Ontario
BACILLARIOPHYTA					
<i>Aulacoseira islandica</i> (O. Müll.) Simonsen	0	6,310	0	0	0
<i>Cyclotella comensis</i> Grun.	2,282	1,915	14,190	30,850	4,142
<i>Cyclotella comta</i> (Ehr.) Kütz.	21,871	193	6,852	116	4,608
<i>Cyclotella delicatula</i> Hust.	8,637	271	1,617	0	945
<i>Cyclotella ocellata</i> Pant.	1,154	74	1,593	40,522	347
<i>Cyclotella operculata</i> (Ag.) Kütz.	1,008	0	0	0	0
<i>Fragilaria crotonensis</i> Kitton	3,898	11,932	6,408	61,089	36,247
<i>Urosolenia</i> spp.	1,139	1,449	442	1,381	178
<i>Synedra filiformis</i> Grun.	40	1,046	1,387	10,740	45
CHLOROPHYTA					
<i>Cosmarium depressum</i> (Nag.) Lund	876	0	132	802	10,732
<i>Cosmarium</i> spp.	161	0	1,955	8,042	0
<i>Crucigenia quadrata</i> Morr.	395	0	0	293	0
<i>Eudorina elegans</i> Ehr.	0	0	0	5,372	0
<i>Golenkiniopsis</i> spp.	50	598	40	2,177	0
<i>Monoraphidium minutum</i> (Nag.) Kom.-Legn.	229	1,509	985	8,663	26
<i>Mougeotia</i> spp.	0	0	0	7,068	0
<i>Oocystis borgei</i> Snow	1,818	0	1,307	1,143	25,723
<i>Pandorina morum</i> (Muell.) Bory	0	0	0	5,709	0
<i>Pediastrum simplex</i> (Meyen) Lemm.	0	0	0	87,160	0
<i>Pediastrum</i> spp.	0	0	0	63,732	0
<i>Planktonema lauterborni</i> Schm.	0	12,933	0	0	0
<i>Quadrigula lacustris</i> (Chod.) G.M. Sm.	0	0	0	937	0
<i>Scenedesmus ecornis</i> (Ralfs) Chod.	41	236	88	926	20,225
<i>Sphaerellopsis</i> spp.	0	0	0	856	0
<i>Sphaerocystis schroeteri</i> Chod.	78	0	0	0	6,477
<i>Staurastrum gracile</i> Ralfs	0	0	0	0	42,877
<i>Staurastrum paradoxum</i> Meyen	0	0	0	0	15,756
<i>Staurastrum</i> spp.	0	0	0	0	12,335
<i>Tetraedron minimum</i> (A. Braun) Hansg.	164	22	31	0	23,912
<i>Ulothrix</i> spp.	308	0	0	834	6,421
<i>Westella</i> spp.	123	691	57	424	1,071
CHRYSTOPHYTA					
<i>Chrysosphaerella longispina</i> Laut. emend. Nich.	910	4,472	70,186	459	0
<i>Chrysosphaerella</i> spp.	0	13,085	382	583	0
<i>Dinobryon bavaricum</i> Imhof	16,025	5,431	12,081	3,967	0
<i>Dinobryon bavaricum</i> var. <i>vanhoeffenii</i> (Bachm.) Krieg.	6,169	0	0	0	0
<i>Dinobryon divergens</i> Imhof	7,189	8,724	6,260	10,938	25,374
<i>Dinobryon sociale</i> Ehr.	3,657	1,229	2,424	3,573	315
<i>Dinobryon sociale</i> var. <i>americanum</i> (Brunnth.) Bachm.	1,881	3,526	756	4,094	154
<i>Dinobryon sociale</i> var. <i>stipitatum</i> (Stein) Lemm.	1,936	358	90	14	0
<i>Dinobryon</i> sp. #1	535	0	655	2,181	0
Haptophyceae	2,465	7,129	5,090	8,692	9,179
<i>Mallomonas</i> spp.	260	3,853	6,168	2,847	1,494
<i>Ochromonas</i> sp. - ovoid	2,904	2,325	4,239	7,017	2,245
<i>Rhizochrysis</i> spp.	1,746	4,239	4,819	5,118	664
<i>Spiniferomonas</i> spp.	885	703	1,932	8,958	0
Unidentified chrysophyte flagellate#4	469	581	3,278	2,751	80
CRYPTOPHYTA					
<i>Cryptomonas erosa</i> Ehr.	4,748	23,515	12,045	19,021	44,073
<i>Cryptomonas erosa</i> var. <i>reflexa</i> Marss.	3,906	5,838	6,501	8,169	17,801

(Continued)

TABLE 2. Continued.

	Superior	Michigan	Huron	Erie	Ontario
<i>Cryptomonas marssonii</i> Skuja	1,702	3,939	372	1,118	2,464
<i>Cryptomonas obovata</i> Skuja	0	0	761	428	0
<i>Cryptomonas ovata</i> Ehr.	389	662	1,236	3,478	19,879
<i>Cryptomonas reflexa</i> Skuja	769	0	1,820	7,292	4,394
<i>Rhodomonas minuta</i> Skuja	8,630	6,933	8,316	21,605	39,086
<i>Rhodomonas minuta</i> var. <i>nannoplanctica</i> Skuja	1,928	6,103	4,289	29,602	32,213
CYANOPHYTA					
<i>Anabaena flos-aquae</i> (Lyngb.) Breb.	0	0	1,335	0	4,588
<i>Aphanocapsa delicatissima</i> W. & G.S. West	2,051	13,067	1,932	8,287	1,694
<i>Chroococcus limneticus</i> Lemm.	0	1,612	1,532	3,690	14,604
<i>Microcystis aeruginosa</i> (Kütz.) emend. Elenkin	341	0	756	3,890	0
<i>Microcystis elachista</i> (West & West) Star.	578	533	585	3,563	0
<i>Microcystis</i> spp.	0	0	0	39,437	0
<i>Oscillatoria</i> spp.	222	0	53	3,673	0
EUGLENOPHYTA					
<i>Trachelomonas</i> spp.	0	0	1,318	0	0
PYRROPHYTA					
<i>Ceratium hirundinella</i> (O.F. Müll.) Dujardin	0	0	18,740	20,337	161,822
<i>Glenodinium</i> spp.	783	0	0	987	13,749
<i>Gymnodinium</i> spp.	2,729	11,763	1,906	6,367	1,234
<i>Peridinium</i> spp.	1,908	11,010	13,405	1,990	66,610

TABLE 3. Average cell counts (#/mL) of *Cyclotella* species in each of the Great Lakes during the summer survey. Results from the individual basins of Lake Erie are presented separately.

Species	Superior	Michigan	Huron	W. Erie	C. Erie	E. Erie	Ontario
<i>C. atomus</i>	0.8			18.5			
<i>C. comensis</i>	15.4	42.0	217.0	125.6	817.5	304.6	65.2
<i>C. comensis</i> var. #1	6.4	57.6	67.4	13.8	505.0	308.4	
<i>C. comta</i>	9.3	0.2	3.8		2.7		2.1
<i>C. comta</i> var. <i>oligactis</i>	2.3				1.3	1.6	
<i>C. delicatula</i>	54.4	13.5	17.0				8.6
<i>C. krammeri</i>	2.2				3.7		
<i>C. meneghiniana</i>	0.6	1.0	1.9	71.4	1.2		2.6
<i>C. michiganiana</i>	2.1	2.8	4.5	2.2	9.9	20.0	0.2
<i>C. ocellata</i>	15.0	1.9	17.8	457.8	638.5	16.1	3.3
<i>C. operculata</i>	5.3						
<i>C. operculata</i> var. <i>unipunctata</i>	1.0				13.9		
<i>C. pseudostelligera</i>	57.3	13.5	54.6	62.1	106.7	188.1	3.5
<i>C. spp.</i>	2.4	0.1	1.3	4.9	4.6	11.2	
<i>C. sp. #1</i>	0.8		0.3	1.7	0.5		
<i>C. stelligera</i>	3.3	0.7	3.4	1.7	5.0	4.7	
Total	179	133	389	760	2,110	855	86

(1988) have documented increases in cyanophyte populations during summer in the nearshore regions of southeastern Lake Michigan from 1974 to 1981.

Fahnenstiel and Scavia (1987) suggested a further change in Lake Michigan phytoplankton communities in the 1980s, specifically a shift toward

phytoflagellate dominance in summer. They presented data indicating that during 1982, 1983, and 1984, mid-stratification communities were comprised of 55%, 91%, and 68% phytoflagellates, respectively. Diatoms during these years usually constituted less than 15% of phytoplankton carbon,

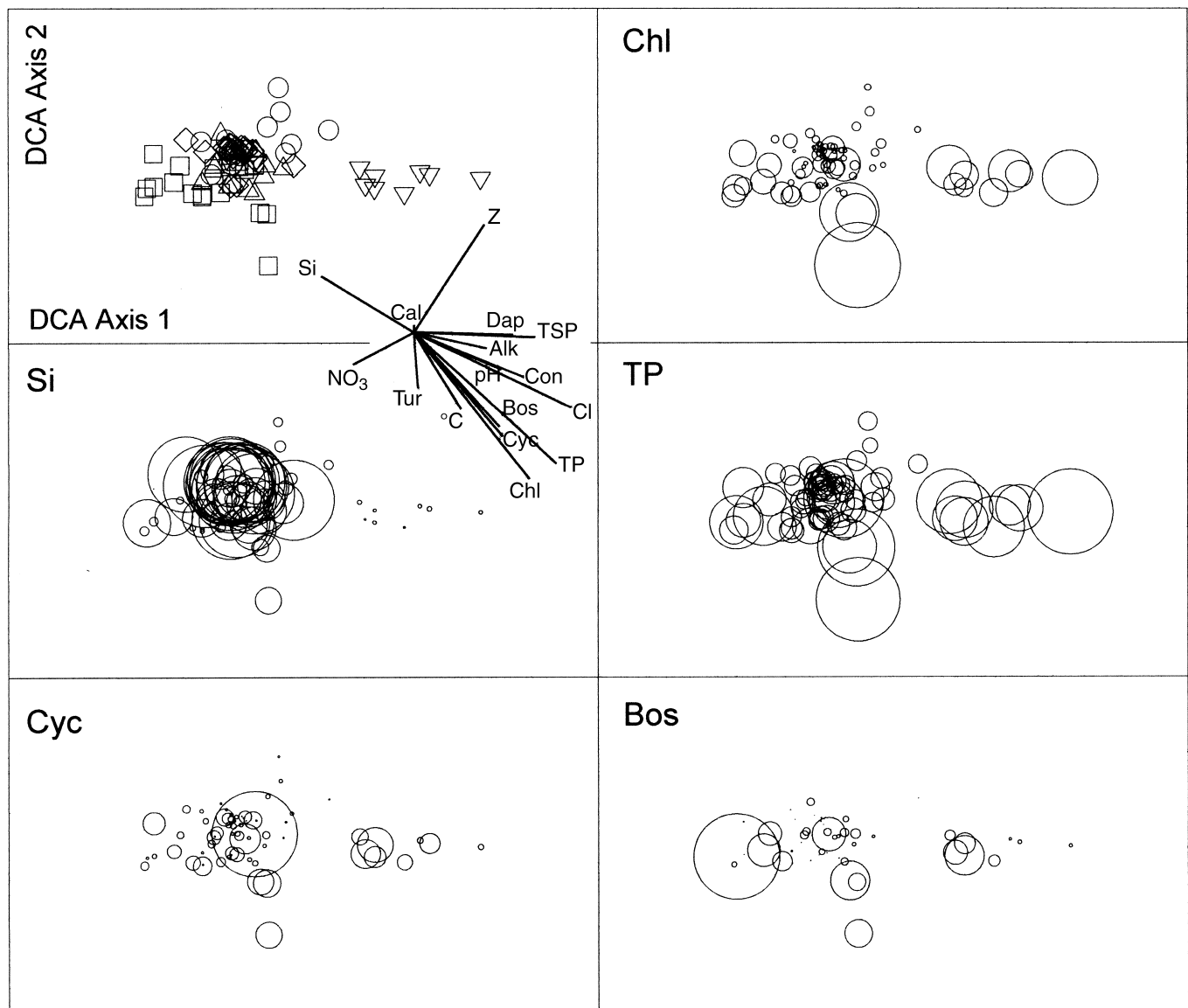


FIG. 11. Results of detrended correspondence analysis (DCA) of summer 1998 phytoplankton data (\diamond = Superior; \circ = Michigan; \triangle = Huron; \square = Erie; ∇ = Ontario), and DCA results with site scores sized according to selected environmental variables. Inset shows correlations of environmental variables with ordination axis scores. The angle of the line indicates the degree of correlation with the two axes, and the length of the line indicates the strength of that correlation. Bos = percent of crustacean community comprised of bosminid cladocerans; Dap = percent of crustacean community comprised of daphnid cladocerans; other abbreviations as in Figure 7.

while the combined contribution of chlorophytes and cyanophytes was 32% in 1982, and less than 4% in 1983 and 1984. However, contrasting results were obtained from a 1982 cruise with extensive spatial coverage, which showed diatoms dominant during both spring (May sampling) and summer

(July and September), contributing about 70 and 50% of the biomass during those two periods, respectively (Munawar and Munawar 1986). The data obtained during this study lend support to the hypothesis that phytoflagellates now dominate the summer community in Lake Michigan; diatom bio-

mass during summer was quite low in this study (app. 10%) while both cryptophyte and chrysophyte biomass was high.

Like Lake Superior, there are few historical data on Lake Huron phytoplankton. There are apparently no quantitative reports of open water phytoplankton communities prior to the 1960s (Davis 1966). Munawar and Munawar (1975, 1982, 1986), reporting on data collected throughout the lake in 1971, found that diatoms never made up less than 80% of the phytoplankton biomass in the northern offshore waters, and were dominant in southern offshore waters until June, when they were replaced by cyanophytes. Munawar and Munawar (1982) pointed out that phytoflagellates were less important in Lake Huron than in the other great lakes. Schelske *et al.* (1974) also found that diatoms were dominant in the open waters of western Lake Huron in September, 1972, with species of *Cyclotella* and *Fragilaria* most prominent. Stoermer and Kreis (1980) found diatoms dominant in the open water of the lake from May through July, 1974, at which time the proportion of cyanophytes and chlorophytes increased. It should be noted they reported cell numbers rather than biomass. Makarewicz and Bertram (1991) presented data generated by GLNPO from 22 cruises undertaken between 1983 and 1985, and compared it with data collected in the 1970s. Like the previous authors, they found diatoms were overwhelmingly important in the lake, constituting 60 to 70% of overall biomass during the course of the study. While chrysophytes made up about 30% of biomass in September 1985, they were otherwise unimportant, and contributed only 9% to overall biomass during the study period. These reports contrast with those of this study, which indicate that in August, chrysophytes were the dominant form, and diatoms a minor component of the plankton. In this study, the relative abundances of major taxonomic groups in Lake Huron were very similar to those seen in Lake Michigan. As noted above, Lake Michigan was historically dominated by diatoms in all seasons, but since the 1980s has been consistently dominated by phytoflagellates during the summer. It is unclear, therefore, whether the similarity in phytoplankton communities between the two lakes in 1998 was anomalous, or indicative of a change in the summer phytoplankton community in Lake Huron towards the more "disturbed" community currently seen in Lake Michigan.

Quantitative studies on the open water phytoplankton of Lake Ontario prior to the 1960s were rare, but point to dominance by diatoms, in particu-

lar *Tabellaria*, *Fragilaria*, and *Melosira* (Davis 1966). There are also early reports of large cyanophyte populations in summer (Tucker 1948). A series of papers on data collected in the early 1970s (Munawar and Nauwerck 1971; Munawar *et al.* 1974; Munawar and Munawar 1975, 1982, 1986) reported that diatoms were abundant through June, with *A. islandica* cited as a dominant species. Summer dominance was variable, with substantial contributions to biomass by cyanophytes, chlorophytes and dinoflagellates recorded during the 3 years examined. Stoermer *et al.* (1974) have also remarked upon the variability of summer communities in this lake. Gray (1987) presented similar results from 1982, noting the absence of several eutrophic diatom species, including *Melosira binderana* (= *S. binderanus*), *S. tenuis*, and *S. hantzschii* var. *pusilla* reported as common in the early 1970s. These reports are largely in keeping with our observations: a spring diatom community overwhelmingly dominated by *A. islandica* leading to a mixed community composed primarily of chlorophytes, cryptophytes, and dinoflagellates. As in 1982, formerly common eutrophic *Stephanodiscus* species were a minor component of the spring phytoplankton community, accounting for less than 0.2% of the spring biomass in this study. A notable aspect of the summer community is the relative paucity of *Cyclotella* species, as was pointed out by Stoermer *et al.* (1974). This genus is characteristic of oligotrophic systems (Foged 1954, Hutchinson 1967) and a substantial contributor to summer communities at most sites in the other Great Lakes. *Urosolenia*, another genus typical of the offshore waters of the Great Lakes, and found in the other four lakes, was almost entirely absent from Lake Ontario.

The phytoplankton of Lake Erie are perhaps the best studied of all in the Laurentian Lakes. Early reports indicated that, at least into the early 1950s, winter, spring and summer communities were dominated by diatoms, with *Dinobryon* often also an important component of summer communities (Davis 1966). In the 1950s and 1960s, the importance of dinoflagellates, cyanophytes and chlorophytes increased (Verduin 1960; Davis 1962, 1964), particularly in the western basin, and cyanophyte blooms were occasionally seen (Tiffany 1958, Casper 1965). Summer dominance by non-diatoms, in particular chlorophytes and cyanophytes, has continued into the 1970s (Gladish and Munawar 1980, Munawar and Munawar 1982). More recently, Makarewicz (1993) has reported reductions

in the biomass of the eutrophic indicator species *Stephanodiscus tenuis*, *S. hantzschii*, *S. binderanus*, and *S. niagarae* between 1983 and 1987, compared to 1970, and the return of mesotrophic species, such as *Asterionella formosa* and *Urosolenia eriensis*, arguing that this indicated a major improvement in the offshore waters of Lake Erie. However, these reductions seemed to be largely due to an overall decrease in biomass, rather than any changes in species dominance. In this study *S. niagarae*, *S. binderanus*, *S. tenuis*, and the closely related *S. parvus* comprised four of the five most abundant species in the central basin of Lake Erie during the spring, although biomasses were substantially lower than were reported by Munawar and Munawar (1976) for 1970. *Asterionella formosa* and *U. eriensis*, while present at some sites, were rare, with the exception of a large population of *A. formosa* in the western basin in the spring. The data do confirm the large reductions in biomass reported by Makarewicz from 1983 to 1987, compared to values from 1970 and 1978. In fact, values for 1998 are lower than most of those reported from the 1980s, arguing for continued improvement in Lake Erie waters, in spite of the continued dominance of eutrophic indicator species. Also notable is the presence of a large and diverse *Cyclotella* flora during the summer (see Table 3). Paleolimnological studies (Stoermer *et al.* 1996) have shown a recent resurgence in populations of this genus in the central basin of Lake Erie, and this was interpreted as evidence of continued recovery of the lake.

Ordination Analyses

DCA results suggest that phytoplankton communities are not determined entirely—or even primarily—by trophic conditions of the lakes; communities often did not align themselves along gradients of nutrients or productivity. For instance, in the spring the eutrophic western basin of Erie was closer in ordination space to the upper lakes than the eastern basin was, and Lake Ontario communities were closer to Lake Superior than to the slightly more productive Lakes Michigan and Huron. Communities in the different lakes were most successfully distinguished in the spring, when all lakes except Lakes Michigan and Huron formed easily recognizable groups. This could have been a consequence of the greater phytoplankton diversity in the spring. It is interesting to note that, while Lake Erie was clearly separated from all other lakes, it also occupied a larger area in ordination space than all the other lakes combined,

indicating both its distinction from the other lakes and the inter-site diversity of its phytoplankton communities.

In both seasons, Lake Ontario communities were most easily distinguishable from all other communities by the ordination analysis, suggesting that this lake supports a distinctive flora relative to the other lakes. It is notable that communities in this lake appeared to be no more similar to those in Lake Erie than communities in the upper lakes were. The unique position of Lake Ontario in ordination space appeared to be most closely associated with its low silica levels in both seasons, and the composition of its zooplankton community, particularly in spring.

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